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Morphology and Taxonomic Position of Podura aquatica (Collembola)

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The morphology of *Podura aquatica* Linnaeus 1758 has been studied, and it has been attempted to single out synapomorphic characters enabling a location of this species within the order Collembola. It is concluded that Podura (for which the subordinal name Metaxypleona has been revived) is the sistergroup of Symphypleona + Neelipleona (inclusive of the Mackenziellidae).

1 Introduction

Podura aquatica Linnaeus 1758 is a common Holarctic springtail, that lives on the surface of stagnant bodies of fresh water. Especially during the summer it can be seen in large numbers in sheltered corners of ditches and ponds. The habitat of the species, its black colour and comparatively large size (1.5 mm) make it a rather conspicuous animal. Its wide distribution may be partly explained by its large tolerance towards water temperature and pH [von Heyner 1972]. It feeds by grazing bacteria and algae from the water surface.

Podura aquatica is one of the best known and most distinctive Collembola [Christiansen & Bellinger 1980]. It has been claimed that some of its characteristics, such as the epicuticular structure [Dallai & Malatesta 1973] and the caput posture [Yosii 1961], are to be considered as strongly primitive. The taxonomic position of the species has varied widely.

The genus *Podura* Linnaeus 1758, once containing all Collembola known to Linnaeus and his contemporaries, includes now the species *aquatica* only. In the first quarter of this century Börner [1913] divided the non-globular Collembola, the Arthropleona, in the Poduromorpha and the Entomobryomorpha. By successive removal of well-defined groups from the Poduromorpha, *Podura* subsequently became the typical genus of a heterogenous group of left-overs. This rather sloppy taxonomy was unfavourably bestowed with a strong persistence and respectability by its acceptance in Gisin's classical Collembolenfauna Europas [1960]. After the familia (or perhaps better familiae) of the Neanuridae had been removed from the Poduromorpha, it has become customary to regard, by elimination of alternatives, the genus *Podura* sensu stricto the sister group of the Hypogastruridae.

Most authors presently consider *Podura aquatica* to be the only representative of a familia on its own. 2 other enigmatic genera, *Actaletes* Giard 1889, and *Mackenziella* Hammer 1953, each usually located in a separate familia are sometimes brought into connection with the Poduridae. Salmon [1964] placed *Podura* in a separate subordo,

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the Metaxypleona, mainly on account of the posture of the caput, which can be regarded intermediate between pro- and hypognathous.
It seemed at the outset that at least some of the characters used to characterize the Poduromorpha might be primitive, rather than derived, and that the group might therefore be less well-founded than it seemed. It turned out, moreover, that *Podura aquatica* might be well-known, but certainly is badly treated in descriptive literature; the best description available is that by Christiansen & Bellinger [1980].

The provision of a fuller description, exemplified with some drawings, and a taxonomic reappraisal of this springtail species is the first aim of the present paper. The main goal of this study has been to unravel the phylogenetic relationships of the Poduridae. Outgroup comparison and ontogenetic studies have been the most important tools in establishing putative apomorphies.

2 Material

Freshly collected adult specimens of *P. aquatica* were used, originating from the Pyrenees. Juveniles were reared in a population that originated from near Amsterdam. Groups of 10–15 adults were kept in small glass jars with a few cm of water partly covered with duckweed. A reed stalk of about 8 cm was placed obliquely in the jar. Jars were covered with plastic foil and kept under room conditions. Dry aquarium fish food was supplied. Oviposition occurred within the reed stalks, which enabled an easy isolation of the eggs. Juveniles, killed immediately after eclosion were considered first instars [L_1][1]. The material was fixated in isopropanol-mixture [von Törne 1965], cleared in chloral-lactophenol, and mounted in Marc André II.

3 Description

The integument has been studied by Dallai & Malatesta [1973], and we refer to their publication for a description and photographs. There are no anal spines. No trace has been found of tracheae.

3.1 Caput. – The caput is held in an oblique prognathous position. The eye counts 8 ocelli and bears 3 setae. Medio-anteriorly the eye-patch bears a more or less spine-like structure (Fig 16). Neither adults nor juveniles have a trace of a postantennal organ.
The labrum has 3 rows of setae: P5, M5, A4. This is different from the observation by Yosii [1961]: P5, M4, A4. Yet, the observation of some asymmetries suggests that this pattern is not very stable (Fig 9). The labral edge is irregularly undulating and bears secondary papillae (not figured). The labium has not been studied in detail, but has the normal appearance of several series of setose papillae that occurs in most groups of Collembola.
The mandibula has a strong molar plate (Fig 7), the caput of the maxilla is lamellate with a reduced number of denticles on the lamellae. There is 1 sublobal seta. [Fjellberg in litt and in press].
The dorsal cephalic chaetotaxy (Fig 1) is difficult to homologize with exisisting schemes, in particular that by Cassagnau [1974], because of extra setae in the dorsolateral field and between the eyes. Compared to the hypothetical, *Hypogastrura*-like, ancestral chaetotaxy [Cassagnau 1974] the vertical and cervical rows are reduced. The chaetotaxy of the L_1 is essentially similar, only the number of setae is somewhat smaller. The distal antennal segments are somewhat fused. The antennal organ III does not offer peculiarities. Sense hairs on ant. 4 are hardly distinguishable; apically there are some sensillae (Fig 6, 8).

[1] first instar, first larval instar; in further text: L_1

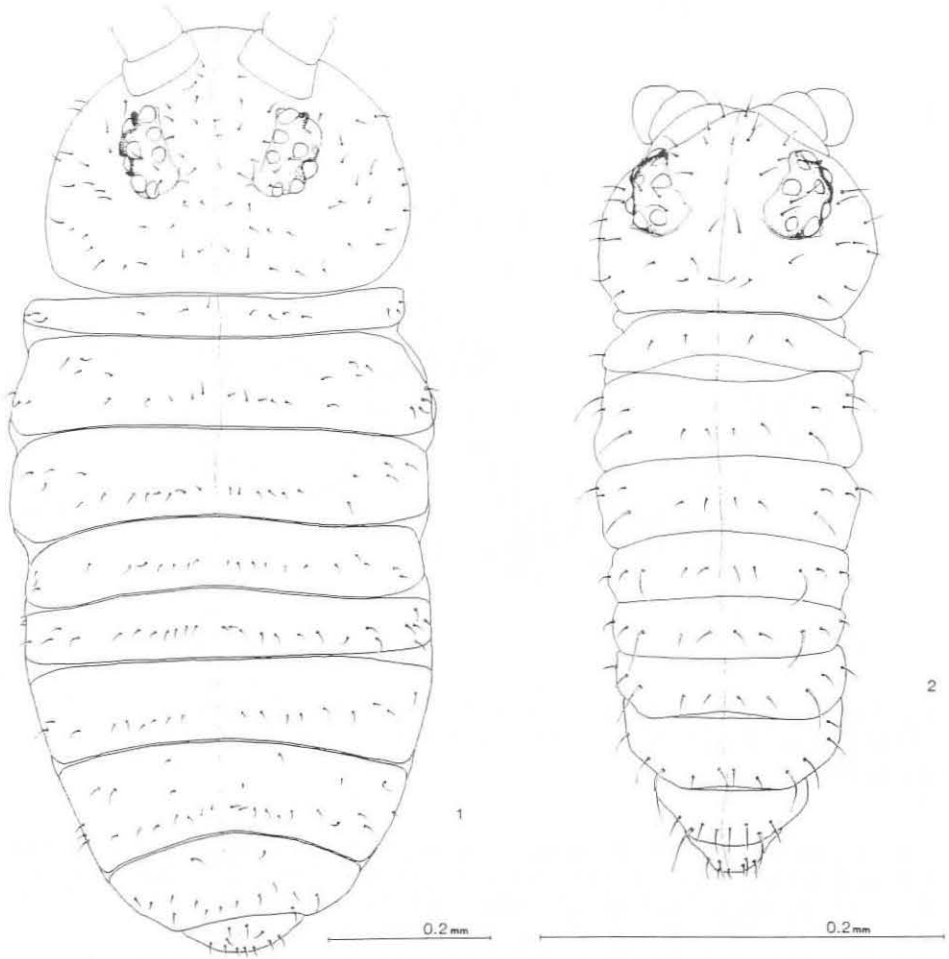

Fig 1–2: Dorsal chaetotaxy of the Springtail species *Podura aquatica* Linnaeus 1758 [Collembola: Metaxypleona: Poduridae]. – 1 imago (composite of 2 specimens: head + body), 2 first instar [L_1].

3.2 Dorsal chaetotaxy. – All thoracal segments and abdominal segments 1–3 have only one transverse row of setae. Only in the abdominal segments 4–6 there are a few setae anterior to the transverse row. These are considered as the remnants of an a-row and an m-row, and the complete transverse row must be homologized with the p-row of Hypogastruridae and Neanuridae s.l. This differs somewhat from the chaetotaxy figured by Yosii [1961].

In the L_1 juvenile only the p-row is present, although with a lesser number of setae (Fig 2). The most lateral seta of the p-row on th2–3 and abd1–5 is much stronger than the median setae of that row. This difference gradually lessens in the course of the ontogeny. These setae, presumably the 'sense hairs', can be homologized with p6 on th2, p8 on th3, p7 on ab1, p8 on abd2, p7 on abd3–4 and p3 on abd5 of the adult's p-row. In all segments they remain the most lateral setae of the adult's p-row. All other setae are unspecialized, and rather short. Asymmetries do occur rather frequently.

Fig 3–5: Pedes of the Springtail species *Podura aquatica* Linnaeus 1758 [Collembola: Metaxypleona: Poduridae]. – **3** pes prothoracalis, **4** pes mesothoracalis, **5** pes metathoracalis.

3.3 Pedes. – The ventral lamella of the long and slender unguis has a minute tooth. The unguiculus is absent. The praetarsus bears 2 setae (Fig 3, 4, 5). The praecoxa of P1 does not bear setae, but is provided with a lobe on its anteroventral face. The subcoxa bears one seta. The coxa has an oval smooth area that might represent an oval or campaniform organ. Both the praecoxa and the coxa of P2 bear one seta, and the anteroventral lobe is present, though much lower. Here also the coxa has an 'oval organ'. Praecoxa and coxa of P3 have a seta as in P2. There is neither a lobus praecoxalis nor an 'oval organ' on the coxa. Tibiotarsal tenent hairs are only weakly differentiated, least developed in P1; they are not clavate.

3.4 Abdominal appendages. – The ventral tube is low, and has no exsertile part. It consists of a basal body and 2 membraneous saclike structures and bears 2 groups of (4–5) setae (Fig 17). The retinaculum is simple, without setae or appendages on the corpus; the rami are quadridentate (Fig 10).

The manubrium is distally cleft, and is setose on its posterior face only. There are no manubrial teeth or comparable structures at the manubrium-dens junction. Basally the manubrium bears 2 short cuticular clasps. These articulate with the basal plate [Manton 1972, von Christian 1979]. On the "basal rods" there is a pair of globular structures, possibly condyles (Fig 14). The dentes are long, tapering, and curved clasper-like in the plane of the manubrium. The distal half bears a series of warty rings. Only the posterior face bears setae. There is a basal group of 4 setae, a median group of 11 setae and a distal group of 2 setae. The integumental annulation is present already in the L_1, but the

number of setae is lower (Fig 12). In juveniles the dental setae are relatively much longer than in the adults, like the lateral setae of the p-row in the dorsal body chaetotaxy.
The mucro has an elongated central body and 4 lamellae (Fig 18–20). The lateral lamellae are broad and limp, which gives them a very variable aspect. At the base of the mucro there is an anterior short lamellose ridge, which may be referred to as a "heel" (Fig 13). The secondary granulation of the dens extends on the central body. There is no mucronal seta.

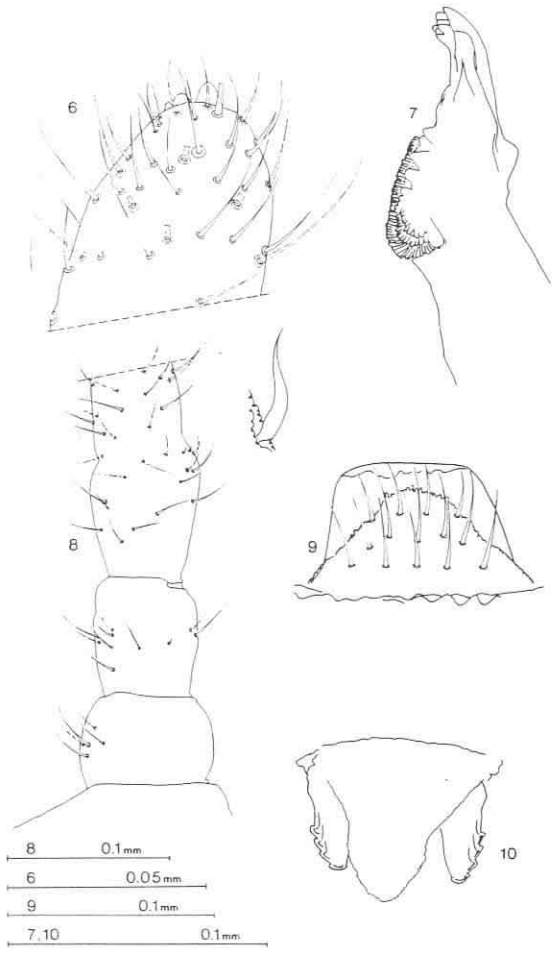

Fig 6–10: Caput and body parts of the Springtail species *Podura aquatica* Linnaeus 1758 [Collembola: Metaxypleona: Poduridae]. – **6** apex of antennal segment-4, **7** mandibula, **8** antenna, **9** labrum, **10** retinaculum.

3.5 Genitalia. – The female genital orifice is a simple transverse slit with anteriorly 3 + 3 setae. The male genital orifice has a somewhat coarser secondary granulation and some 6 + 6 unspecialized setae. For a description of the inner genitalia we refer to Schliwa [1965].

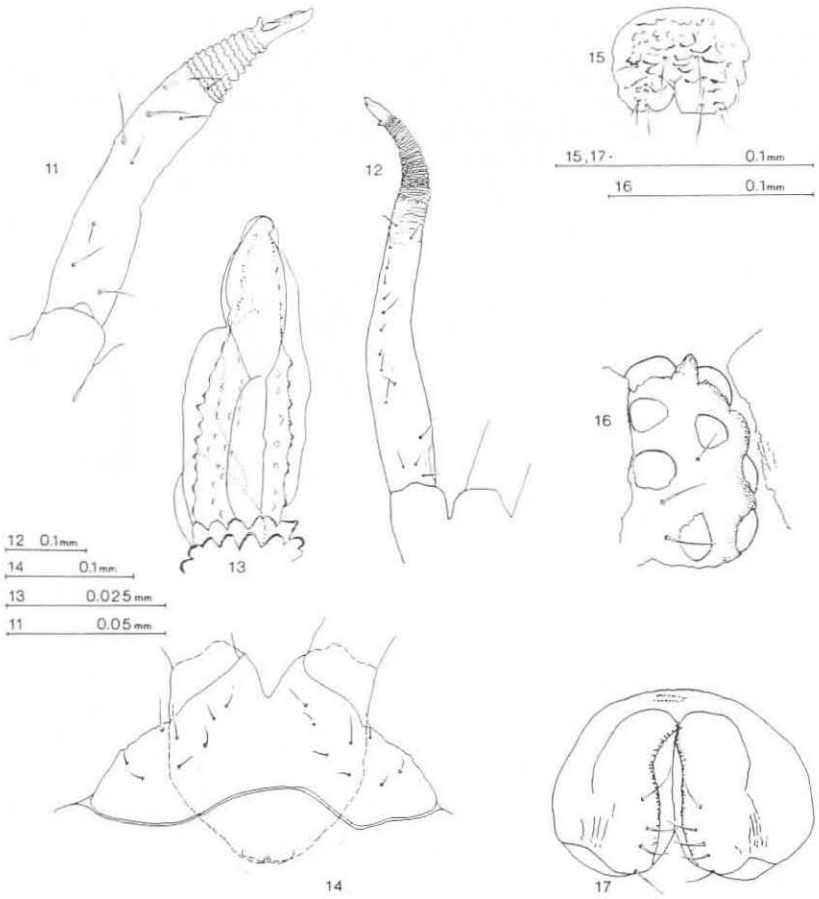

Fig 11–17: Caput and body parts of the Springtail species *Podura aquatica* Linnaeus 1758 [Collembola: Metaxypleona: Poduridae]. – **11** dens of juvenile, **12** dens of adult animal, **13** mucro (adult), **14** manubrium in rest position (dotted line indicates the end of the basal rods), **15** male genital papilla, **16** eye patch, **17** tubus ventralis.

4 Character analysis

4.1 Primitive characters

4.1.1 Prothorax. – The fact that the prothorax of *Podura* is well developed, and even setose, must be regarded as a primitive character since this is the situation that occurs in the Protura and Diplura – and in almost all Ectognatha for that matter. This implies that the 'higher Collembola' may well be characterized by the reduction of the prothorax. Of course, the characterization of the Poduromorpha on the strength of the primitive condition cannot be maintained.

4.1.2 Body chaetotaxy. – The chaetotaxy of the other body segments is very peculiar. If we would base ourselves on straightforward outgroup comparison of adult specimens, we would be forced to the conclusion that the body chaetotaxy is derived, and the result of an extreme reduction. Yet, this is far from confirmed by the ontogeny. Here we see that the few traces of the a and m-row present in the adult animal originate in the course of the development. As a general rule, character states that occur early in the ontogeny are primitive as compared to the states later in the development [Nelson & Platnick 1981]. The view that a single transverse row per segment is primitive is corroborated by the serial homology with the obvious plesiomorphic situation in the prothorax. If this view is correct, *Podura* would present the most original chaetotaxy of all Collembola.

4.1.3 Caput posture. – The slightly hypognathous position of the head stands in obvious connection with the way food is grazed from the water surface. Because the situation in *Podura* is barely, if at all, different from the primitive prognathous caput position of non-Symphypleona and other Endognatha, there is no reason to build taxonomic conclusions on this character.

4.1.4 Cuticula. – As stated already by Lawrence & Massoud [1973], the epicuticular ornamentation cannot considered as derived either.

4.1.5 Other characters. – The structure of ventral tube, retinaculum, mouthparts, labrum and labium reflects that of the large majority of all Collembola, and is thus clearly primitive by outgroup comparison.

4.2 Derived characters

4.2.1 Lack of postantennal organ. – A postantennal organ [PA][2] occurs in a large number of Collembolan groups – if we are indeed justified in considering the PA of Sminthuridae as homologous to that of Isotomidae etc. In the Tomoceridae a PA occurs only in very young specimens. We therefore regard the absence of the PA in *Podura* to be a derived character.

4.2.2 Precoxal process. – The precoxal lobe of P1 und P2 immediately brings in mind the so-called 'subcoxal' spur of *Anuridella* Willem 1906 (Anuridae) and the precoxal process of P1–3 that is widely distributed among the Symphypleona [Richards 1968, Betsch 1980].
Anuridella is totally unrelated to *Podura*, and belongs to a well-defined familia; it seems justified to conclude that its subcoxal spur represents an autapomorphy.
Because precoxal spurs are not known to us outside of the Collembola, their shared occurrence in Poduridae and Symphypleona hints to a meaningful synapomorphy. (This suggestion may be refuted, however, if it could be demonstrated that the precoxal processes are homologous with the coxal vesicles of Onychophora. Boudreaux [1979: 147] seems to accept this).

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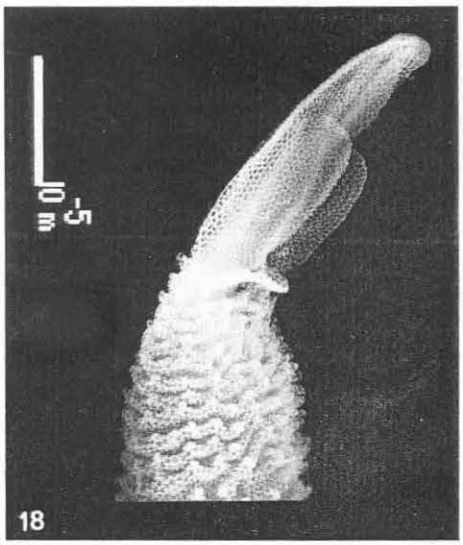
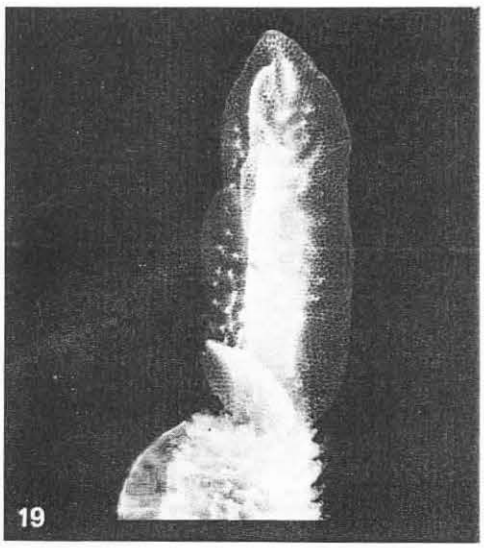
[2] postantennal organ = organum postantennalis; in further text: PA

4.2.3 Oval organs. – If the cuticular modifications of the coxae of P1 and P2 are oval organs indeed, they may well be homologous with the oval organs that occur on the praecoxae of P2 and P3 in the Bourletiellidae and Sminthuridae, and on the tibiotarsus in another familia of Symphypleona, the Sminthurididae [Betsch 1980].

4.2.4 Unguiculus. – The total reduction of the empodium is an apomorphic character. But the loss of the unguiculus clearly has occurred independently in several groups, and the value of the character must be rated rather low.





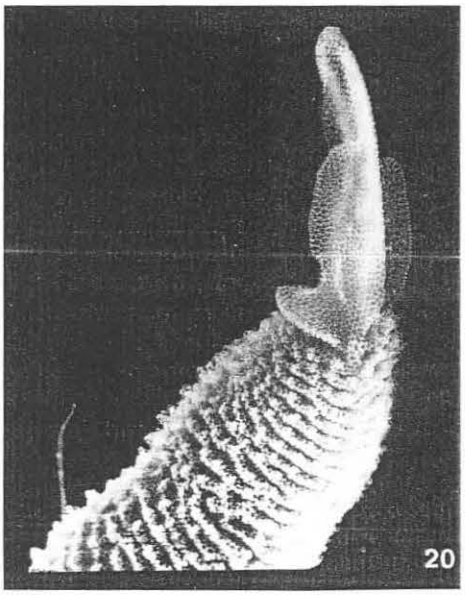


Fig 18–20: Mucro (in 3 different views) of an adult specimen of the Springtail species *Podura aquatica* Linnaeus 1758 [Collembola: Metaxypleona: Poduridae].

4.2.5 Manubrium. – The furca shows some of the most rewarding details. The distal cleft of the manubrium represents a situation that otherwise is known only in the Sminthuridae, as was noticed already by Yosii [1961], and in the Neelipleona.

4.2.6 Condyles. – The so-called condyles at the manubrial plate are shared by the Symphypleona and Neelipleona that we checked for the character. Only a study specially devoted to this structure will disclose if this is a useful apomorphy.

4.2.7 Dens. – The peculiar curvature of the dens is an autapomorphy that well suffices to isolate *Podura* from all other Collembola.

4.2.8 Mucro. – The complex, lamellate mucro in itself easily reminds one to the Symphypleona, in particular the Sminthuridae. It reflects in almost all details the hypothetical mucro of the ancestral Symphypleona drawn by Richards [1968]. In particular the basal structure called here 'heel' seems to have its counterpart in the mucro of most Sminthuridae. *Podura* does not have a mucronal seta, a character that was considered by Richards to be part of the mucro of the ancestral Symphypleona. That, however, was refuted already by Betsch, wo draw attention to the fact that the mucronal seta is never present in the L_1, even in those species where it is present in later stages.

5 Neelidae and Mackenziellidae

In the lines above the implication was reached that Poduridae shared the highest number of synapomorphies with the Symphypleona. Before a definite statement about their relationship can be made, it is necessary to take into account 2 familiae that are traditionally loosely connected with the Symphypleona.

Neelidae are not well-known, morphologically, because of their minute size, and but three specimens are known of *Mackenziella psocoides* Hammer 1953, the only species of the Mackenziellidae. Although it is therefore rather premature to speculate about the position of these familiae, some facts may be brought forward that at least suggest their taxonomic place within the Collembola.

First, contrary to Hüther [1964], we agree with Paclt [1956] that Neelidae and Mackenziella are closely related. Shared apomorphies that indicate this are: their minute size, relatively large thorax, fused abdominal segments, large unguicular tubercle (in almost all Neelidae), very long sense hairs on ant.4, presence of 'Kehltuberkel' in the prosternum (e g drawn for *Megalothorax gabonensis* by Massoud & Vannier 1965); finally, in Hüther's drawings there is a suggestion of a branching of the linea ventralis between pro- and mesosternum, a character that has its parallel in the branching below the caput in *Megalothorax* Willem 1900 and *Neelus* Folsom 1896 [Deharveng 1979] and the sternum in *Neelus* [unpubl]. We conclude therefore that Neelidae and Mackenziellidae form a monophyletic group, and we propose to enlarge the concept of the Neelipleona to accomodate both familiae.

Second, we believe that the Neelipleona form a monophyletic group with the Symphypleona. This is based on two synapomorphies:

(a) The tendency of the body to become globular – although realized differently in Neelipleona and Symphypleona. In the Symphypleona it is mainly the abdomen that has lost most of its segment limits and is strongly enlarged; in the Neelipleona it is the thorax that forms the major part of the body. The globular shape is weakest in *Mackenziella*, but

even here there is a tendency to an obliteration of segment limits, and to enlarge the thoracal segments.
(b) The presence of a neosminthuroid seta [Betsch 1980] both in Neelidae, drawn for instance for *Neelides folsomi* Caroli 1912 by Dallai [1979], and in the Symphypleona. Whether it is also present in *Mackenziella* is not known.
Finally, we argue that the Neelipleona + Symphypleona together form the sistergroup of the Poduridae because of 4 putative synapomorphies shared by the 3 groups:
(1) Neelidae have a precoxal process, at least clearly visible on P1 of *Neelus*. (No data for *Mackenziella*, possibly absent). (2) The 'condyles' of the basal rods of the manubrium are present in *Neelus* Folsom 1896 (we have no data for *Mackenziella*).
(c) The manubrium of Neelidae is cleft, as in Poduridae and the Symphypleona (again no hard data on *Mackenziella*, albeit a suggestion in Hüther's mentioning a ventral longitudinal furrow).
(d) The absence of a postantennal organ.
It may be considered a contra-indication that no 'oval organs' are seen in the Neelipleona. But, apart from mere problems of observation power, there is the added problem that Neelidae (perhaps also *Mackenziella*) have grossly enlarged, obviously strongly transformed coxae.
It must be remarked, moreover, that if this cladogram is correct, we must face the corollary that the mucronal 'heel' of Symphypleona and Metaxypleona either constitute 2 independant developments or is lost secondary in the Neelipleona.

6 Conclusion

There is, among the characters that have been analyzed in the present study, no synapomorphy that would suggest a close relationship of *Podura* with the Hypogastruridae. On the contrary, the conclusion is inescapable that despite the low number of useful characters, all indications point towards a close relationship of the Poduridae with the Symphypleona and the Neelipleona.
To give the Poduridae a taxonomic status equivalent to the one of its sistergroup, Neeli-

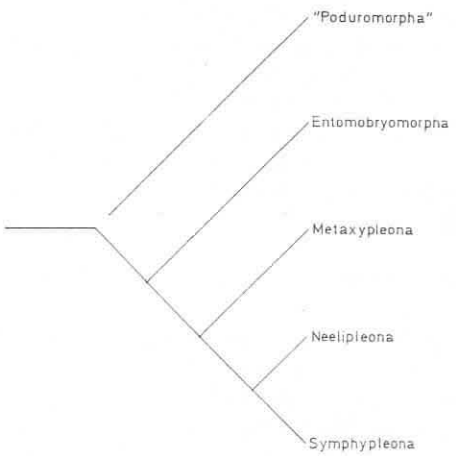


Fig 21: Scheme of phylogenetic relationships in Collembola, including the systematic position of Poduromorpha.

pleona + Symphypleona, it is proposed here to revive the name Metaxypleona Salmon 1964. The sistergroup of the whole complex is formed by the 'Arthropleona' [Fig 21].

Summarizing our results, we find that we should divide the ordo Collembola into 5 groups. The first consists provisionally of Hypogastruridae + Neanuridae s.l., and no synapomorphies are known for it; its sistergroup, the 'higher Collembola' is characterized by the reduction of the prothorax. The 'higher Collembola' in turn are divided into the Entomobryomorpha and its sistergroup, Metaxypleona + Neelipleona + Symphypleona.

This puts an end to the long-established name Poduromorpha, not because of nomenclatural laws, but because Poduromorpha after exclusion of the Poduridae would be a nonsensical name. Since it remains to be established if the Hypogastruridae s.l. and the Neanuridae s.l. together form a natural group we propose no new name to replace the Poduromorpha. The name Arthropleona, designating a paraphyletic group of Hypogastruridae/Neanuridae + Entomobryomorpha, must be abandoned anyway.

Christiansen & Bellinger [1980] rightly said that *Podura aquatica* is the most distinctive of all species of Collembola. It is the sole survivor of one of the main stems of Collembola. Not the least remarkable fact is that *Podura aquatica* is restricted to the Holarctic, whereas its sistergroup is pandemic.

7 Acknowledgements

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